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ON XEROPHYTIC ADAPTATIONS OF LEAF STRUCTURE IN YUCCAS, AGAVES AND NOLINAS[1]

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ZOOLOGY and botany are now so separated, and for a worker in one field to venture into the other is so unusual that it may not be out of place to state my reasons for presenting this paper, which are as follows:

1. Practically all of the material was worked up in 1903–4, and since I shall not have opportunity to complete the study I wish to make this part available.

2. I wish to emphasize the importance of the results of plant physiology to the zoologist. Many of those phenomena now brought into such prominence in zoology (*i. e.,* trophisms, heteromorphosis and the mutually antitoxic action of sodium and calcium) were discovered in plants and later studied in animals. Likewise the study of the water economy of desert plants may ultimately throw some light on similar processes in animals that are subjected to constant (*i. e.,* Dermestes) or periodic lack of water (*i. e.,* rotifers). The cutin of plants and the chitin of animals play similar rôles, and it may be that the carbohydrate and mucoid (?) water-storing substances in plants have analogues in animals.

I am indebted to Dr. W. L. Bray for suggesting and directing this study, and for procuring the material, most of which he obtained from Langtry, Texas and from the Missouri Botanical Garden.

Methods.—The most serviceable method for investigating cell walls was free-hand sections stained in chloriodide of zinc. A freezing microtome might have been of service. Celloidin did not penetrate thoroughly in six weeks and was abandoned. Thin paraffine sections were cut, but where bundles were isolated in succulent tissue they usually tore through part of the latter. The experimental side of the subject was not touched.

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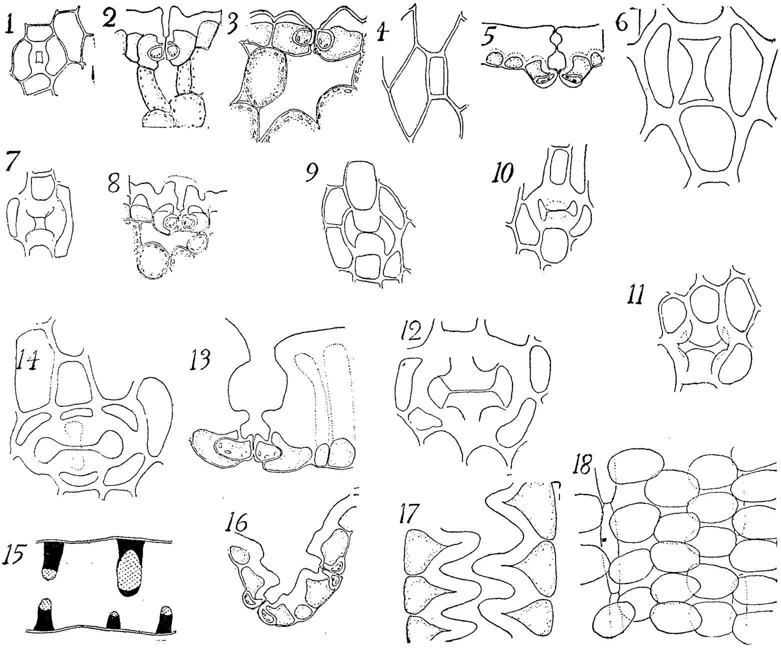
[1] Contribution from the Botanical Laboratory of the University of Texas under the direction of Dr. W. L. Bray.

Yucca and its allies are mostly xerophytic plants that have been modified along various lines to adapt them to their xerophytic habitat. Root, stem and leaf are succulent, thus serving for water-storage tissue. The leaves are closely set in a rosette, thus protecting one another against too great insolation and transpiration. In Agave, Hesperaloe, Dasylerion, Nolina and some species of Yucca the stalk is very short, thus enabling the leaves to shade the ground over the larger roots and protect them from drying. The leaves are especially modified: the epidermis is greatly thickened and heavily cutinized, the skeleton more or less rigid, the stomata sunken beneath the surface, either singly or in grooves, and the assimilation tissue many layers thick.

The Respiration System.—The simplest type of stoma in this group is probably found in *Yucca aloifolia tenuifolia* (Figs. 1 and 2). In this species the guard cells are not sunken much beneath the general epidermal surface, but the very thick epidermis is pierced by an air passage nearly square in cross section (Fig. 1), leading to the slit between the guard cells. Beneath the guard cells is an intercellular air space of considerable size leading into small intercellular air spaces. The epidermis is heavily cutinized and the cutin extends inward through the stoma and lines the upper part of the air space beneath. The assimilation tissue is palisade near the epidermis; but the cells show a tendency to arrange themselves radially around the vascular bundles. There are large intercellular air spaces in the interior of the leaf. Stomata of like character were found in *Yucca aloifolia, Y. aloifolia marginata, Y. aloifolia conspicua, Y. gloriosa* and *Y. gloriosa flexilis.*



(In diagrammatic cross sections mechanical tissue is black and vascular tissue cross striated.)

Fig. 1. Stoma of *Yucca aloifolia tenuifolia*—surface view.
" 2. The same in cross section of leaf.
" 3. Stoma of *Agave yuccæfolia* in cross section of leaf.
" 4. Same—surface view.
" 5. Stoma of *Dasylerion texanum* in cross section of leaf.
" 6. Stoma of *Agave americana*—surface view.
" 7. Stoma of lower side of leaf of *Yucca recurvifolia*—dotted lines represent portions of two teeth that are covered by the other two.
" 8. Same in cross section of leaf.
" 9. Stoma of *Yucca radiosa*—surface view.
" 10. Stoma of *Y. rostrata*—surface view—passage beneath teeth shown by dotted line.
" 11. Stoma of *Y. glauca*—surface view.
" 12. Stoma of *Agave victoria reginæ*—surface view.
" 13. Stoma of same in cross section of leaf.
" 14. Stoma of *A. schotti*—passage beneath teeth shown by dotted line.
" 15. Diagram of part of cross section of leaf of Nolina sp.? from Mexico.
" 16. Groove in cross section of leaf of *Dasylerion glaucophyllum*.
" 17. Groove in tangental section of leaf of *Nolina texana*.
" 18. Assimilation tissue in longitudinal section of same.

In *Agave yuccæfolia* the cutinized layer of the epidermis is thinner and the air passage leading to the stoma proper is much shorter than the preceding and is elongated parallel to the long axis of the leaf (Figs. 3

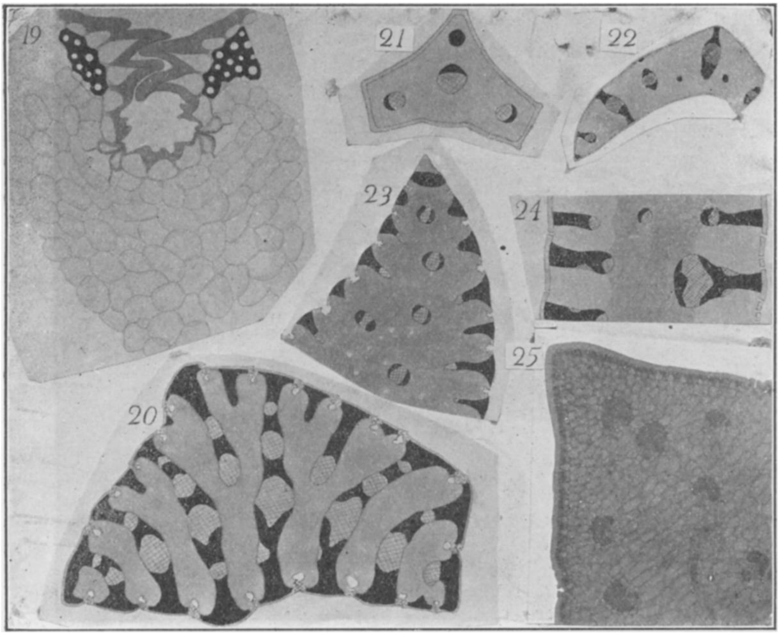


FIG. 19. Groove in cross section of same—the cutinized portion of epidermal cell walls shown darker than other cell walls; mechanical tissue black.
" 20. Cross section of leaf of same.
" 21. Cross section of leaf of young seedling of same.
" 22. Same after two years growth in damp greenhouse.
" 23. Part of cross section of leaf of *Hesperaloe parviflora*.
" 24. Part of cross section of leaf of *Dasylerion wheeleri*; the middle of the leaf is filled with large celled storage tissue.
" 25. Part of cross section of leaf of *Agave strida*—photograph.

and 4). Beneath the cuticle is a thick layer of water-storing cellulose. A series of forms with this type of stoma arranged in order of progressive sinking of the stoma would include: *Hesperaloe præciosa, Yucca de smetiana, Y. rupicola, Agave strida* and *Dasylerion texanum.* In the last named (Fig. 5) the supra-stomal passage is divided into two dead air spaces, and the stomata occur in slight longitudinal furrows. The ridges between are braced heavily with mechanical tissue.

In *Agave americana,* the century plant (Fig. 6), the sides of the elongated supra-stomal passage are produced into lips, constricting it in the middle.

In *Dasylerion wheeleri* a second similar constriction occurs half way down this passage, so that in cross section it appears like *Dasylerion texanum.* In this species the epidermal cells are produced into papillæ.

Going back to the simple type of stoma found in *Yucca aloifolia* we can trace variation in another direction. In the stomata of the lower side of the leaf of *Yucca recurvifolia* the four sides of the supra-stomal passage are produced into lips; those parallel to the long axis of the leaf being beneath the others (Figs. 7 and 8). On the upper side of the leaf the lips are not as well developed, and are all in the same plane, as are also those of *Yucca australis* and *Y. treculiana.*

In *Yucca radiosa* (Fig. 9) and *Y. constricta* only two of the lips are developed, so that we have an opening somewhat like the ones in *Agave americana* rotated through a right angle. In *Yucca rostrata* the lips have developed so as to close the opening in the middle, leaving only an opening at each end (Fig. 10).

In *Y. glauca* (Fig. 11) four additional lips have developed above the two as in *Y. radiosa,* and the accessory cells have sunken considerably beneath the level of the other epidermal cells.

In *Agave victoria regina* (Fig. 12) the presence of six lips is accompanied by the meeting of one pair and by the division of the supra-stomal passage into two dead air spaces (Fig. 13). Here the epidermal cells secrete an immensely thick layer of reserve or water-storing (?) cellulose under the cuticle (Fig. 13). The leaf is very succulent and the vascular bundles are confined to the middle layer.

In *Agave schotti* the shape of the supra-stomal passage changes greatly as we go inward. On the surface it is elongated at right angles to the long axis of the leaf, while farther down it is elongated parallel to the long axis (Fig. 14).

Besides being sunken singly between the level of the epidermis the stomata are often placed in rows at the bottom of a groove. These grooves are very slight in Nolina sp.? from Mexico (Fig. 15), *Dasylerion wheeleri* and *D. texanum.* They are deeper in *D. glaucophyllum* (Fig. 16) and *Hesperaloe parviflora.*[2] They are very deep and guarded with teeth in *Nolina texana*[3] (Figs. 17 and 18) and Nolina sp.? from West Texas. The formation of grooves is directly associated with the bracing of the epidermis with beams of mechanical tissue (Fig. 20) along the ridges between the grooves. In Nolina sp.? from Mexico (Fig. 15), *Dasylerion wheeleri* (Fig. 24), *D. texanum* and *Hesperaloe parviflora* (Fig. 23) these beams are free in the interior of the leaf, but in *D. glaucophyllum* and *Nolina texana* (Fig. 20) the beams of one side usually meet and fuse with those of the other, forming a rigid support for the epidermis that prevents any dorso-ventral shrinkage of the leaf on drying. The only shrinkage that does occur closes the grooves and thus is a further check to transpiration. Another characteristic associated with the presence of these longitudinal transpiration grooves is a peculiar modification of the air passages in the assimilation tissue, which reaches its greatest development in the Nolinas. In the forms without grooves there is an irregular air space below the stoma, from which lead minute air spaces in all directions. With the development of grooves is associated a more effective arrangement of these air spaces, so that rapid respiration of the deeper tissue is effected without the devotion of much of the volume of the leaf to air space. If we imagine the groove represented in Fig. 17 in tangential section, as being placed horizontally with the opening upward, the assimilation tissue in the form of lamellæ one cell thick is suspended from the inner surface of the groove. Air diffusing in through the stomata enters the narrow spaces between the lamellæ and almost immediately penetrates to the center of the leaf. If we

[2] Bray, '03.

[3] Bray, '03.

imagine a lamella removed from the leaf when turgid, the cells composing it would be rounded on their free surfaces. If such a lamella were placed on another so that some of its cells rested on the apices of the cells of the one underneath, we should get a condition similar to that in *Nolina texana* (Figs. 18 and 19) and allied forms. Fig. 18 is drawn from a thick longitudinal section of the leaf, and the irregularities in the lamellæ obscure their distinctness. The lamellæ are additionally supported by columns of elongated cystoliths running parallel to the long axis of the leaf and connecting one lamella with another.

Mechanical and Vascular Tissue.—The leaves of Yucca and its allies are covered by a very thick cutinized epidermis which is quite stiff and supports the soft tissue beneath, thus forming an exoskeleton. In smooth leaves the bundles are distributed through the interior of the leaf, in thick leaves being arranged in several rows (Fig. 25). Each bundle is composed of vascular tissue supported by a large amount of mechanical tissue, and thus the bundles form an internal skeleton. In those leaves in which grooves occur the ridge between two grooves is heavily braced within with mechanical tissue (Fig. 23). These braces often extend inward until each fuses with a bundle (Fig. 23) and in some species all the bundles are attached to the inner edges of these braces (Fig. 15). In *Dasylerion glaucophyllum* and some species of Nolina (Fig. 20) the braces of one side of the leaf usually fuse in the middle with those of the other side, making a very rigid structure.

Relation of Habitat to Structure of Stoma.—The complexity in structure of stoma in these forms lead Dr. Bray to suggest that I see whether there was any correlation between the structure of the stomata and the aridity of habitat. I found that there was in all except those that had the supra-stomal passage much elongated in the long axis of the leaf. *Yucca aloifolia, Y. gloriosa* and their varieties have a supra-stomal passage nearly square in cross section (Fig. 1) that goes straight down to the stoma, and these species inhabit coast lands which, although hot, are humid. In *Y. australis, Y. treculiana* and *Y. recurvifolia* the supra-stomal passage is guarded by four lips (Fig. 7) and these species inhabit a region from the Gulf coast to the dry interior of the United States and Mexico. In *Y. radiosa* and *Y. constricta* the supra-stomal passage is closed in the middle (Fig. 9) and these species inhabit southern Arizona, western Texas and adjacent country. In *Y. rostrata* two widely separated openings lead into the supra-stomal passage (Fig. 10), and we find this plant in the deserts of northern Mexico. In *Agave victoria regina* we find a similar structure with the addition of four small lips (Fig. 12) and we find this plant also in the deserts of northern Mexico (Coahuila). In *Yucca glauca* we find a structure similar to the preceding save that the two lower lips are slightly separated (Fig. 11), and this plant inhabits the slightly less arid lands from South Dakota to New Mexico and North Texas. In *Agave schotti* the supra-stomal passage is compressed in one axis (Fig. 14) and a little lower down is compressed at right angles to the first (Fig. 14, dotted line) and we find this plant in the deserts of southern Arizona. Finally, the Nolinas, whose stomata are placed in deep grooves guarded by interlocking teeth, cling to crevices in the rocks in western Texas and northern Mexico, where not only is the air dry and the sun hot, but there is extremely little soil to hold a store of moisture.

Development of Leaf in Nolina Texana.—The very young leaf in the adult plant is not deeply grooved as in Fig. 19 or 20 and the mechanical tissue is not well developed. The formation of grooves is associated with the formation of ribs of mechanical tissue supporting the epidermis between the bands of stomata, and by growth inward uniting with the vascular bundles, thus forming girders extending through the leaf in a dorso-ventral direction. The epidermis bulges out along the lines of attachment of the girders and sinks in between them. The epidermal cells bordering the grooves thus formed grow out into long interlocking teeth. The teeth get longer and the groove narrower as the leaf develops, thus protecting the stomata from the dry air.

In the very young seedling the leaf is somewhat triangular in cross section (Fig. 21) with a vascular bundle in the center and one in each lateral angle and a bundle of mechanical tissue in the midrib. The epidermis is cutinized at this early stage.

I kept a seedling in a greenhouse of the University of Pennsylvania about two years. The leaves did not grow stout as in plants from the natural habitat and I think the increased moisture and diminished insolation affected the thickness of the leaves (Fig. 22). The leaves were very thin; the mechanical tissue uniting with the vascular bundles formed beams connecting the dorsal with the ventral epidermis between the bands of stomata, but the grooves only began to develop. It seems remarkable that a plant so adapted to xerophytic conditions should be able so quickly to adjust itself to a moist atmosphere, and I think the subject merits further investigation.

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